

**PARASITE-HOST INTERACTIONS
IN AN ARCTIC GOOSE COLONY**

A Thesis

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By

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ABSTRACT

The arctic is currently experiencing some of the greatest rates of warming. Newly emerging diseases in the arctic are of particular interest due to the implications these may have at southern latitudes if temperatures continue to rise around the globe. It is important to document changes in pathogen populations, such as alterations in range, virulence, prevalence, and abundance, and the effect these may have on their host populations. Parasites influence the reproductive success of their hosts in some cases. Studies on impacts of ectoparasites on avian reproductive success have generally been focused on species with altricial young. I studied the abundance of an apparently newly emerging nest-parasite and the effects of this parasite on Ross's (*Chen rossii*) and lesser snow goose (*Chen caerulescens caerulescens*) reproductive success in the Karrak Lake goose colony, Nunavut, Canada from 2001 to 2004.

The nest parasite, identified as the flea *Ceratophyllus vagabundus vagabundus*, was associated with goose eggs covered with spots of blood. The proportion of goose egg-shells covered by blood was positively correlated with flea abundance in the nest. This relationship allowed the use of egg blood-coverage as an index of flea abundance for remaining analyses. Flea abundance in goose nests was associated with variables associated with the host and the host's habitat. I used general linear models in conjunction with Akaike's information criterion (AIC) to determine which factors were most important in influencing flea abundance in goose nests. The most parsimonious model to explain the relationship between egg blood coverage and flea abundance in goose nests included goose clutch size, age of nest bowl (new vs. old), history of nesting by geese on a specific plot within the colony, habitat within 0.5m of nest, and year. The

best predictor of flea abundance was the age of the nest bowl, with nest bowls re-used by geese containing more fleas than new bowls. This relationship was expected as fleas over-wintered in goose nests at the Karrak Lake colony.

Logistic regression and AIC were used to determine whether egg blood-coverage was an important variable influencing nest success. All top five models included blood-coverage. Goose nest success was negatively influenced by fleas in most years. There was a threshold of egg blood-coverage at which nest success was affected, and this threshold varied, with >20% blood indicating a significant decline in nest success in two years, and >5% blood-coverage indicating a decrease in nest success in one year. To my knowledge, this is the first study that has examined the parasites of avian nests in an arctic ecosystem and was also the first to investigate the effect of nest parasites on birds with precocial young. More research is needed to determine what factors limit this flea population and whether fleas may become a regulating factor for geese in the Karrak Lake colony.

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DEDICATION

This thesis is dedicated to my parents, Valerie and Jim. Their support, love, and understanding have never faltered. Thank-you.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 INTRODUCTION

Parasitism is an ecological association between species in which the parasite lives on or inside the host. The parasite detrimentally impacts its host from which it obtains nutrients (Anderson and May 1978). Parasitism is likely the most common feeding strategy (Sukhdeo and Bansemir 1996). Parasitic insects (or ectoparasites) constitute 10% of animal diversity (Askew 1971).

Anderson and May (1978) raised awareness within the scientific community to the importance of parasite population biology. Like most organisms, parasite distribution is spatially complex likely due to gradients in resource quality and availability. It has long been accepted that parasites are highly aggregated (Crofton 1971, Anderson and May 1978, Poulin 1993) and discussions of why parasites occur where they do have been ongoing in parasitology (Sukhdeo and Sukhdeo 1994, Sukhdeo and Bansmir 1996, Krasnov et al. 2003). It is important to study the population dynamics of parasites, not only for the benefit of gaining knowledge related to parasite populations, but also because we may then have more insight into effects of parasites on host populations. Hosts are an integral part of parasite life cycles. Host behavior and abundance is influenced by and influence parasite populations (Anderson and May 1978). As we cannot gain full understanding of parasite populations without considering

their hosts, we also cannot fully understand host population dynamics without consideration of their parasites.

Parasite-host interactions are important ecological processes that can have large evolutionary consequences on host dynamics and life history strategies (Ewald 1983, Begon et al. 1990, Clayton et al. 1999). Parasites employ a variety of strategies in order to successfully manipulate host populations and so enjoy persistence. Negative impacts on host reproductive success have been linked to parasite abundance, particularly in populations of song birds (see Richner et al. 1993, Fitze et al. 2004, O'Brien and Dawson 2005).

Populations of Ross's (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*) have been growing rapidly likely due to the release from previously regulating factors. About 90% of the world's population of Ross's geese and 15% of lesser snow geese nest in the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS; Drake and Alisauskas unpublished data). Within the QMGMBS, the Karrak Lake colony is among the largest (Alisauskas et al. 1998).

Eggs covered in blood were detected in 1991 in some nests in the colony at Karrak Lake (W. Sturgeon personal communication). It wasn't until 1997, when this phenomenon became more common, that observers also noted the presence of fleas. The prevalence and intensity of blood-covered eggs in the colony appeared to increase between 1991 and 1997, with as much as 100 percent of some eggs being covered with blood by 1997. This blood was subsequently hypothesized to result from fleas feeding on incubating female geese causing bleeding on eggs, and/or from fleas regurgitating or defecating undigested blood on goose eggs.

Diseases, particularly those which are newly emerging, can grow at near exponential rates (Akçakaya et al. 1999). It is possible that populations of parasitic fleas on geese may increase with consequences on nesting success and fitness of host geese. Populations are likely regulated by density-dependent factors. We would expect new limiting factors to arise in populations that have been released from previously regulating factors (Begon et al. 1990). It is suggested that Ross's and snow goose populations have increased in response to landscape changes (Alisauskas et al. 1988; 1998), and are no longer limited by food resources. Fleas may potentially play a role in the regulation of goose populations through a reduction in goose reproductive success. The Karrak Lake goose colony presents an ideal opportunity to study nest parasites of colonial, arctic nesting geese, as well as the influences these ectoparasites may have on the population dynamics of the geese.

1.2 THESIS OBJECTIVES

The general objectives of my thesis were as follows:

- 1) To determine the relationships between blood coverage on eggs and flea intensities on Ross's and lesser snow geese and in their nests. Adult fleas are known to defecate undigested blood to provide food for their larvae; however, egg blood-coverage has never been reported in this magnitude. It was therefore necessary to provide an index of blood-coverage to flea numbers.
- 2) To investigate factors influencing flea abundance within goose nests. Factors

considered included two categories, the host (species, clutch size, nest initiation date) and the host's nest and surroundings (habitat, nest bowl age, history of nesting on plot, host densities).

- 3) To evaluate the relative importance of fleas on goose nest success. Results of previous studies analyzing the effects of parasites on avian reproductive success have been mixed.
- 4) To identify patterns between proportion of eggs covered by blood and goose nest success. This objective allowed me to determine whether different intensities of fleas disproportionately influenced nest success.

1.3 STUDY AREA

This study was conducted at the Karrak Lake goose colony (67°14'N, 100°15'W), located ~60 km south of Queen Maud Gulf, Nunavut, in the QMGMB (Figure 1.1).

The QMGMB was established in 1961 under the Migratory Birds Convention Act of 1917 to protect nesting birds. The goose colony encompasses about 360 km², of which 200 km² is terrestrial habitat, including rock outcrops and sedge meadows (Ryder 1972).

Geese have altered much of the vegetation within the colony (Alisauskas et al. 2006).

The Karrak Lake colony has grown rapidly in the last decade, increasing from an estimated 426,000 geese in 1993 to 960,000 in 2003 (Alisauskas unpublished data).

During 2001-2004, annual nest density averaged 22-34 nests/ha with a range of 0-250 nests/ha (Alisauskas unpublished data). Other bird species nesting within the goose

colony include: Glaucous gulls (*Larus hyperboreus*), Herring gulls (*Larus argentatus*), Arctic terns (*Sterna paradisaea*), Canada geese (*Branta canadensis*), king eiders

(*Somateria spectabilis*), long-tailed ducks (*Clangula hyemalis*), red-throated loons (*Gavia stellata*), Arctic loons (*Gavia arctica*), and red-breasted mergansers (*Mergus serrator*). Arctic foxes (*Alopex lagopus*) are the primary mammalian predators of geese and their eggs in the Karrak Lake colony.

1.4 STUDY SPECIES

1.4.1 Ross's and Lesser Snow Geese

Ross's and lesser snow goose populations have been growing at unprecedented high rates. The Ross's goose population has averaged an annual increase of 11.3% a year since the 1950's. The lesser snow goose population has increased at an average rate of 14.5% a year (Ryder and Alisauskas 1995). This increase is likely partially a result of agriculture expansion. Ross's and snow geese have adapted to utilize agricultural land throughout their migration and on their wintering grounds, resulting in greater nutrient acquisition (Alisauskas et al. 1988)

Most Ross's geese nest in the central Canadian arctic (Ryder and Alisauskas 1995) and many winter in the central valley of California (Turner et al. 1994). Lesser snow geese nest throughout the central Canadian arctic and Hudson Bay, as well as on Wrangel Island, Russia (Kerbes et al. 2006) and winter throughout the Pacific, Central and Mississippi Flyways. Ross's geese usually nest in association with lesser snow geese (Ryder and Alisauskas 1995). Geese arrive on their nesting grounds late May and early June and depart early July, with lesser snow geese typically arriving and initiating nests 2-4 days before Ross's geese. Geese may either build a nest or use an old nest bowl, to which some new nest material and down is usually added. Nests are initiated in

early June, with Ross's and lesser snow geese in the Karrak Lake colony averaging 3.2 and 3.7 eggs respectively (Slattery and Alisauskas 1995). Only one clutch is produced per breeding season (Ryder and Alisauskas 1995) and nests are incubated an average of 23 days (Alisauskas unpublished data). In 1976, nests were a reported 2.8 meters apart on average in the high density areas of the Karrak Lake colony (McLandress 1983). Incubation constancy is high in both goose species, with female Ross's geese attending and maintaining the nest 87% of the time (Afton et al. 1995). Goslings hatch synchronously, are precocial, and leave the nest with parents within 1-2 days.

1.4.2 Siphonaptera

Only 6% of the world's 2,500 species of fleas infest birds (Lehane 2005). Bird fleas reside primarily in the host's nest, only visiting the host for feeding (Marshall 1981). Hatching cues for the fleas are likely provided by geese as they prospect for and build nests and may include vibrations, temperature increases, or increased CO₂ concentrations (Askew 1971, Marshall 1981). After hatching, fleas can go without a blood meal for months. Female fleas require a blood meal to produce eggs which are laid in the host's nest (Lehane 2005). Feeding on non-preferred hosts can severely reduce flea reproduction (Lehane 2005). Flea eggs usually hatch into larvae within two to six days. Flea larvae are rarely parasitic (Boyd 1951), feeding on undigested blood defecated by adult fleas and to a lesser extent on nest cup material. It has been hypothesized that adult fleas may respond to the corticosteroid level in host blood by feeding in excess and increasing their rate of defecation of undigested blood immediately before laying their own eggs for the purpose of providing food for the

larvae (Rothschild and Ford 1966, as cited in Askew 1971). The larval period lasts under a month, after which the larva produces a cocoon in which it will pupate (Lehane 2005). Although the duration of the pupal stage is only a week or less in southern environments, this is the stage in which the fleas over-winter at the Karrak Lake colony (Harriman et al unpublished data). Despite their ability to survive over winter, fleas in the cocoon are highly susceptible to desiccation (Askew 1971, Marshall 1981). New blood is only detected on eggs within the first few days of incubation and continues ~ 4 days into incubation, suggesting that there is likely only one substantial emergence of adult fleas in the Karrak Lake colony.

The nest parasite of geese in the Karrak Lake colony has been identified as the flea, *Ceratophyllus vagabundus vagabundus* (Boheman 1866). There are 22 species in the genus *Ceratophyllus*, all of which infest birds (Lewis and Galloway 2001). The distribution of *C. v. vagabundus* is circumpolar in the northern hemisphere, primarily located in mountain ranges inland or along northern coasts and islands (Lewis and Galloway 2001). It is primarily found in association with colonial hosts nesting on the ground or on rock or cliff faces. The principal hosts of *C. v. vagabundus* include gulls, ducks, sea birds, and raptors (Holland 1985 as cited in Lewis and Galloway 2001). This flea has not previously been reported in association with *Chen* spp. The only record of *C. v. vagabundus* associated with a goose is a record from 1925 in which the author noted them in an unidentified goose nest on Spitsbergen (Elton 1925).

1.5 THESIS ORGANIZATION

Although there is anecdotal evidence of fleas depositing small amounts of blood on waterfowl eggs in the prairies, this is the first study directly linking blood on eggs to flea abundance. No nest parasites have been previously reported in association with Ross's or snow geese and additionally, no studies have been conducted on the impacts avian nest parasites in arctic regions. This study is also unique in that parasite abundance was examined as it related to both the host and the host's immediate surroundings. Finally, this research marks the first study of nest parasite effects on an avian host bearing precocial young, and the first on nest parasites of a waterfowl species.

I have organized the thesis into four chapters. Chapters 1 and 4 cover the general introduction and general conclusions, respectively. Chapters 2 and 3 are structured as journal articles. Chapter 2, "The case of the blood-covered egg: factors influencing variation in ectoparasite abundance in an arctic goose colony," addresses objectives 1 and 2 above. Chapter 3, "Of fleas and geese: the impact of an apparently newly emerging disease on reproductive success," addresses objectives 3 and 4.



Figure 1.1. Karrak Lake is the largest goose colony in Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, and consisted of approximately 1,000,000 nesting Ross's and lesser snow geese 2001-2004. Thick solid lines on large map and dotted lines on inset map indicate the boundary of the Queen Maud Gulf Migratory Bird Sanctuary.

CHAPTER 2: THE CASE OF THE BLOOD-COVERED EGG: FACTORS INFLUENCING VARIATION IN ECTOPARASITE ABUNDANCE IN AN ARCTIC GOOSE COLONY

2.1. INTRODUCTION

Populations are generally spatially complex partly due to the heterogeneity of the landscape they inhabit. Parasites are often clumped due to host location and density. Additionally, individuals of these aggregated parasites may be further clumped, as only a few individuals may host many parasites, while most individuals have few or none (Crofton 1971, Anderson and May 1978, Poulin 1993). Like all other parasites, ectoparasites gain their nutrients from a host species. However, ectoparasites live on the outside of their hosts and are therefore influenced by variables external to the host as well as to anti-parasite host defenses such as immune response and preening. Identifying factors influencing ectoparasite abundance includes not only consideration of the host, but also features of the host's habitat. Few studies to date have taken this multifaceted approach when considering parasite abundance (but see Laakkonen et al. 2003).

The Queen Maud Gulf Migratory Bird Sanctuary (QMGMB) in Nunavut, Canada was established to protect nesting birds. Notably, almost the entire population of Ross's geese (*Chen rossii*) and 15% of lesser snow geese (*Chen caerulescens*

caerulescens) nest there (Drake and Alisauskas unpublished data). The Karrak Lake goose colony is one of the largest Ross's and lesser snow goose colonies in the QMGMB (Alisauskas et al. 1998). In 1991, blood-covered eggs were first noted in goose nests by researchers at the Karrak Lake colony. It was not until 1997 that this phenomenon became conspicuous through much of the colony. Subsequently, fleas were noted in association with nests containing blood-covered eggs. The flea, identified as *Ceratophyllus vagabundus vagabundus* (Boheman 1866), had not been previously reported in association with Ross's or snow geese (Harriman et al. unpublished data).

Bird fleas are predominantly found in their host's nest rather than on the bird. Egg, larval, and pupal development usually occur off the host (Marshall 1981). Host blood constitutes the most important part of the diet of flea larvae, and is obtained by consumption of adult flea fecal pellets (Askew 1971). It has been hypothesized that adult fleas feed in excess to their requirements, subsequently defecating undigested blood upon which larvae feed. Adult female fleas may increase their rate of defecation just before laying eggs in response to the corticosteroid level in host blood (Rothschild and Ford 1966 as cited in Askew 1971). The blood observed on goose eggs likely results from fleas feeding on incubating geese, with subsequent defecation in the nest by fleas. I first tested whether there was an association between flea abundance and proportion of eggs covered by blood. I then estimated the strength of relationships between extent of blood on goose eggs and a variety of factors related to hosts and habitat associated with nests of hosts. The objective of this study was to determine whether adult flea abundance in goose nests depended on host features and/or host nesting habitat features.

2.2. METHODS

2.2.1. Study Area

This study was conducted at the Karrak Lake goose colony (67°14'N, 100°15'W) within the QMGMB. The colony encompasses ~360 km², however only ~200 km² is terrestrial habitat. Ross's and lesser snow geese nest at high densities, with the average nesting density of nests during the 2001-04 period of study being 22-34 nests/ha (range 0-250 nests/ha) annually (Alisauskas unpublished data). Geese arrive in the colony in late May, initiating nests in early June. Approximately one egg is laid per day, with an average clutch size of 3, and hatching occurs after ~23 days of incubation (Alisauskas unpublished data).

2.2.2. Fleas in the Karrak Lake Colony

The flea, *C. v. vagabundus*, over-winters as a pupa in a cocoon and emerges each spring with the arrival of geese (Harriman et al. unpublished data). Geese likely provide hatching cues for fleas such as vibration, a rise in temperature, or increased CO₂ concentrations (Marshall 1981). There appeared to be only one major emergence of adult fleas as new blood was detected only within the first few days of incubation and continued ~4 days into incubation. Larvae became obvious in goose nests within ~10 days of incubation by geese. All eggs within a clutch had similar coverage by blood.

2.2.3. Study Design

To determine the relationship between blood-coverage on eggs and flea abundance, birds and nests were collected in two different years. In 2003, Ross's geese and their nests were collected during mid-incubation (16-19 days), and in 2004 geese and nests of both goose species were collected during early incubation (1-4 days). Geese were obtained by shooting with a rifle under permit from Canadian Wildlife Service. Three areas of the colony were chosen for goose collection due to their proximity to a high point from which we could observe birds and geese could be shot. Geese and their nests were chosen for collection based on the proportion of eggs coverage by blood; the goal was to acquire a broad range of blood coverage. Up to a dozen nests were marked with flagging within sight of each other; however, of these only a few could be collected. Geese were shot for collection only if the female had returned to the marked nest and continued incubating. Most females did not return to their nest during observation, and so were not collected. Geese were collected and placed in a bag within 30 seconds of being shot. The proportion of each egg covered by blood was visually estimated for every nest using a standardized visual reference (Figure 2.1) and subsequently averaged over the nest as most eggs in the same clutch had either the same or similar coverage by blood. Birds and nests were double-bagged and then frozen and thawed twice to kill fleas.

All birds ($n = 26$) and nests ($n = 26$) were surveyed systematically for adult fleas. Birds were surveyed at the research station and fleas were placed in ethanol and counted upon return from the field. Birds were placed in ventral recumbency on white paper and feathers were ruffled and searched dorsally from the back of the head to the tail, then

turned over and searched from tail to head on the ventral side. Wings were surveyed last. Average search time for birds was 15 minutes. Nests were transported to Saskatoon for processing. Entire nests were placed on white paper during flea surveys. Small amounts of nesting material were removed at a time, thoroughly searched, and discarded. This was continued until all nesting material had been surveyed. Between 1 and 10 hours were required to search each nest.

Since 1993, nest plots have been used in the Karrak Lake colony to sample nests for estimation of initiation date, clutch size, hatch date, nest success, species composition, and population size of geese in the colony. Many different observers collected data on nest plots each year (up to 20 people/year). This study used nest plot data from 2001-04. Plots were placed systematically throughout the colony on a 1 km by 1 km grid and were marked with a center pole. Within a 30 meter radius around the center marker, each nest was numbered and eggs were marked with unique nest and egg numbers. Length and width of each egg were recorded and the goose species was determined from egg measurements following Alisauskas et al. (1998). Incubation stage was estimated using an egg candler (Weller 1956) and nest initiation date was calculated from incubation stage and clutch size. The proportion of the each egg surface covered by blood was averaged within a nest and recorded. A visual reference was used to improve consistency among observers in 2003-04 (Figure 2.1), but not in 2001-02. Nest bowls were categorized “old” if egg membranes, old down, or old nest markers from nesting attempts made in previous years were present; otherwise nest bowls were classified as “new.” The history of nesting by geese at individual plots was calculated using data from 1966-2004 (Kerbes 1994, Alisauskas et al. 2006). This allowed us to determine how many years specific areas had been used for nesting by geese. Dominant

habitat type within 0.5m of each nest was recorded as: rock, mixed (gravel-filled soil upon which low vascular plants grow sparsely), heath, dwarf birch (*Betula glandulosa*), or moss. Plots were visited once during incubation and each nest was re-visited after eggs hatched. Nests were successful if at least one egg hatched, which was determined by the presence of gosling down, egg cap, and/or egg membrane. Nest density was expressed as the number of nests/plot.

2.2.4. Statistical Analyses

General linear models (PROC GLM, SAS Institute Inc., 2001) were used to examine relationships between blood-coverage on eggs and bird and nest adult flea numbers.

Due to a reduction of blood on eggs and likely death of adult fleas as incubation progressed, data from early and mid-incubation were analyzed separately for both flea numbers on birds and in nests. Additionally, flea numbers in nests were not combined between early and mid-incubation due to differences in flea lifecycle stages found in nests. An analysis of co-variance (PROC GLM) was used to determine whether blood on eggs was related to flea abundance, the incubation stage at which nests were collected at, or an interaction between these variables. Akaike's information criterion adjusted for small sample size and number of parameters (AICc) was used to determine which model best explained variations in egg blood-coverage of collected nests. Five *a priori* additive models were considered.

General linear models were used to determine how proportion of blood on eggs (an index of flea abundance varied in relation to host species, host clutch size, nest initiation date, age of nest bowl, history of nesting on plot, habitat, nest density, and

year. The option ESTIMATE was used for parameter estimation. Incubation stage was rearranged eggs in the nest throughout the incubation period. Density of birds and nest initiation date were positively correlated, and therefore these variables were not included in the same model. No other variables were closely correlated. Twenty *a priori* additive models were considered. Interactions among covariates were not included due to uncertainty of ecological relevance. I used AICc to rank quality of models about variation in egg blood coverage (Burnham and Anderson 2002).

2.3. RESULTS

Number of plots and number of nests examined, prevalence of nests containing blood-covered eggs, and average coverage by blood for the 4 years of study are shown in Table 2.1. The amount of dried blood that remained adhered to surfaces of goose eggs was slowly reduced as geese rolled and rearranged eggs in nests during incubation (Harriman et al. unpublished data). A greater proportion of blood persisted at the poles of the eggs than at the middle, presumably because of less abrasion against other eggs and nest material at the poles. In heavily infested nests, blood remained on egg surfaces at least part of the nesting period, and the poles of eggs in some nests often retained dried blood throughout the nesting period. The proportion of eggs covered by blood were related to the numbers of adult fleas detected on collected birds during early incubation ($F_{1,1}=19.97$, $r^2=0.60$, $P<0.001$), but not during mid-incubation ($F_{1,1}=2.54$, $r^2=0.22$, $P=0.15$). Few adult fleas were detected on birds collected during early and mid-incubation. The number of fleas detected on birds ranged from 0-4. Most birds (65%) had no fleas ($n=17$) and few had 1 ($n=2$), 2 ($n=5$) or 4 ($n=2$) fleas. There were far more

fleas detected in nests (range 0-500). Adult flea intensities in nests were positively related with blood-coverage during both early incubation ($F_{1,1}=66.01$, $r^2=0.84$, $P<0.001$) and mid-incubation ($F_{1,1}=156.12$, $r^2=0.95$, $P<0.001$; Figure 2.2). The model that best explained the influences on proportion of eggshells covered by blood included flea abundance in nests and the interaction between flea abundance and stage of incubation at which the nest was collected ($F_{1,2}=267.36$, $r^2=0.93$, $P<0.001$). This model was the only model with a ΔAICc less than two and held a model weight of 0.80.

The most parsimonious model about influences on flea abundance included 5 of the 8 factors considered: clutch size, age of nest bowl, history of nesting, habitat, and year ($F_{1,11}=31.57$, $r^2 = 0.096$, $P<0.001$; Table 2.2). Parameter estimates of blood-coverage are presented in Table 2.3. Coverage of eggs by blood increased with clutch size in all years ($F_{1,1}=9.91$, $r^2=0.002$, $P<0.01$; Figure 2.3). Age of nest bowl showed the strongest influence on egg blood-coverage ($F_{1,1}=94.83$, $P<0.001$) with eggs in old bowls experiencing greater coverage by blood on average in all years (Figure 2.4). Blood-coverage was greater in older areas of the colony ($F_{1,1}=26.33$, $r^2=0.026$, $P<0.001$; Figure 2.5) in all years. Host nesting habitat significantly influenced proportion of blood-coverage ($F_{1,4}=5.65$, $P<0.001$); nests in rock and birch habitats contained eggs with more blood than other habitat types in all years, whereas nests in heath contained eggs with less blood than other habitats (Figure 2.6). Finally, blood coverage fluctuated annually ($F_{1,3}=29.24$, $P<0.001$; Figure 2.7).

2.4. DISCUSSION

2.4.1. Blood to Flea Index

Blood on goose eggs likely originated from flea feces, and the amount of blood defecated would therefore be proportional to number of fleas. The results showed that the numbers of fleas in nests were closely correlated to egg blood-coverage; however, numbers of fleas on birds were not related to blood on eggs during one of the two years. The numbers of fleas detected on birds were correlated with blood-coverage during early incubation but not mid-incubation. This was similar to findings reported on fleas of the house martin (*Delichon urbica*; Rothschild and Clay 1952), very few fleas were detected on birds relative to nests. This suggests that *C. v. vagabundus* spent more time in nests than on nesting geese at Karrak Lake, and the number of fleas detected on birds was not a reliable indicator of flea abundance throughout the goose incubation period. The number of fleas in nests proportional to blood-coverage differed between early and mid-incubation when an interaction between flea abundance was included. Larvae were not detected in nests collected early in incubation but were abundant in nests collected during mid-incubation, possibly influencing the probability of flea detection probability. Additionally, blood on eggs was reduced as incubation progressed. Therefore, blood-coverage of eggs in the same nest would be scored higher at early incubation than at mid-incubation. Adult fleas were also likely dead by mid-incubation, and due to the fragility of their exoskeletons, were probably not available for collection during this time. More fleas were detected at lower blood coverage during early incubation (Figure 2.1), likely due to the combination of blood reduction on eggs, decreased detection, and the probable death of most adult fleas by mid-incubation.

2.4.2. Host Factors and Flea Abundance

Flea abundance in the Karrak Lake goose colony appeared to be associated with five of the variables measured, only one of which was directly host-dependent. Blood-coverage on eggs and clutch size were positively correlated. Birds that arrive earlier on breeding grounds tend to lay more eggs in many waterfowl species (Reynolds 1972, Krapu et al. 2004). However, because there was no relationship between nest initiation date and blood coverage (and also was not correlated with clutch size), it is unlikely that the difference in blood-coverage in respect to clutch size was influenced by timing of nest initiation by geese. Instead, this pattern is consistent with use of hosts by fleas on the basis of host health. Healthier birds likely lay more eggs (Alisauskas and Ankney 1992) and some parasites prefer better-fed hosts (Dawson and Bortolotti 1997, Christe et al. 2003). Fleas might select for healthier host individuals. Alternatively, fleas might defecate more blood in nests containing more eggs. Nest attentiveness has been related to clutch size with larger clutches requiring higher attentiveness (Blagosklonov 1977 as cited in Deeming 2002, Larsen et al. 2003), thus providing parasitic fleas with a relatively uninterrupted supply of food might allow them to increase defecation frequency or quantity.

Conversely, the apparent use by fleas of nests containing more eggs may have been a response by geese. Fleas emerge before geese lay eggs and infest geese before and/or early in nest initiation. Geese may have responded to fleas by laying more eggs. Larger clutches cool more slowly during incubation breaks (Reid et al. 2000), possibly allowing for longer breaks (Reid et al. 2002). Infested geese may lay more eggs so that they may decrease their attentiveness during early incubation when fleas are most

prominent. However, Ross's and lesser snow geese are likely constrained by the nutrient reserves they arrive on the breeding grounds with (Alisauskas and Ankney 1992). These constraints may prohibit geese from making upward adjustments in clutch size in response to flea numbers.

2.4.3. Host Habitat Factors and Flea Abundance

At the Karrak Lake goose colony, flea abundance was associated with more factors related to host's habitat rather than the host itself. The external environment may be more significant to arctic dwelling ectoparasites than to those in temperate climates due to climatic limitations (Marshall 1981). Flea intensities were higher in old nest bowls. About 50% of geese re-used old bowls during this study. At the Karrak Lake colony, *C. v. vagabundus* over-wintered in goose nests, as is common of *Ceratophyllus* species (Marshall 1981). Fleas likely laid eggs in the nest in which they inhabited and all life cycle stages were completed in the nest with no movement of the flea's offspring being possible until the following year when a new adult flea could emerge from the cocoon. If an infected nest was re-used the following year, it is likely that the fleas emerging in the nest would infect the goose using the nest. Thus, older nest bowls had a greater probability of housing fleas.

Additionally, fleas appeared to be more common in areas of the colony with a longer history of goose nesting. This pattern is likely influenced by dispersal probability of fleas, which is unknown at Karrak Lake. Most fleas are dispersed by their host (Rödl 1979 as cited in Marshall 1981). Visits of 10 seconds by small mammals to their nests were enough for fleas to infect their host; however, up to 50% of fleas in nests were able

to transfer onto the host if it remained in the nest for 1 hour (Rödl 1979 as cited in Marshall 1981). Most geese likely do not spend considerable time in an area they will not nest in. My results suggest that the dispersal and/or establishment ability of fleas in Karrak Lake is limited because nests in newer areas of the colony appeared to be less infested than those in older areas of the colony on average.

Flea intensities varied with habitat surrounding goose nests. These results may be related to spatial patterns of snow accumulation during the winter months and snow melt in the spring. The highest ridges near Karrak Lake are generally windswept and free of snow earliest in the spring. Upland, well-drained areas of the colony tend to be rocky. These upland and intermediate mixed habitats melt earlier than the lowland areas which are dominated by heath and moss habitats (Ryder 1969). Lowland areas are most likely to experience freeze/thaw cycles of runoff during spring. All fleas collected on birds were dead after freezing for a week, subsequently thawing, and freezing again for a week. If fleas emerged in these lowland areas before nesting began, they likely would have not survived continual freezing and thawing. Birch is usually located throughout midland and lowland habitats. However, birch, as well as rock, likely melts earliest in the spring due to heat radiation (Pomeroy et al. 2005). An earlier melt and constant heat radiation likely allows fleas over-wintering in nests in these areas to be free of snow and ice and thus ready to infest geese early in the season, possibly increasing their ability to complete their lifecycle. Snow accumulates around shrubs, increasing insulation and therefore elevating subnival temperatures around shrubs (Sturm et al. 2001). Areas around rocks also accumulate snow in the same manner as shrubs. Fleas are highly susceptible to desiccation in the cocoon (Askew 1971) and therefore this increase in

insulation in conjunction with being comparatively well-drained may be beneficial to the survival of over-wintering fleas.

Flea abundance varied annually. The proportion of eggs covered by blood was highest in 2002. The sample size for this year was much lower than other years, possibly contributing to differences seen in this year. On average, clutch size, age of bowl, history of nesting, and nesting habitat usage were not different than that of the other three years of study. The stage of incubation at which nests were visited was 1.5 days earlier than the average of the other three years. Because incubation stage was controlled for in the model this likely does not completely explain the difference observed. Snow depth was recorded via 12 transects in the colony from late May to early June (during 2001-2004). Snow depth recorded between May 28th and 30th (the earliest date snow depth data was collected in all years) was deeper in 2002 on average than in any other year. Over-wintering fleas may have been better insulated in 2002 than in other years, thus increasing their survival rates.

2.4.4. Implications and Summary

The objective of this study was to determine whether blood on goose eggs was directly related to flea abundance and to assess factors influencing flea abundance in the Karrak Lake goose colony from 2001-2004. The proportion of eggs covered by blood was a good predictor of flea abundance. Flea abundance was associated with both host and host-habitat factors. Of particular interest were those factors that are in part related to flea dispersal abilities, age of nest bowl and history of nesting. *Ceratophyllus vagabundus vagabundus*, has been described as a generalist flea, because it can use a

variety of hosts. Generalist fleas have adaptations allowing for greater mobility than do specialist fleas (Tripet et al. 2002). However, Tripet et al. (2002) also concluded that fleas of colonial nesting birds are usually specialists and are not well adapted to dispersal. The dispersal abilities of *C. v. vagabundus* in the Karrak Lake colony are unknown. However, the flea's life cycle, in conjunction with the fact that it infects colonial nesting hosts, would support the selection of traits which would decrease dispersal.

Warmer arctic temperatures will likely aid the expansion of dwarf birch in the tundra ecosystem (Liston et al. 2002). Because this habitat may be associated with increased flea over-winter survival, this extension may facilitate the expansion of fleas throughout the colony. It is likely that the goose population at Karrak Lake will also continue to grow. An increase in host individuals should lead to an increase in parasite abundance (Anderson and May 1978). It appears that *C. v. vagabundus* is a new parasite of geese at the Karrak Lake goose colony and that flea abundance may change in response to the increased availability of variables influencing flea fitness as time progresses with potentially important implications for flea population dynamics, and perhaps for flea speciation.

Table 2.1. Number of plots and nests observed, prevalence of nests containing blood-covered eggs, and average egg blood-coverage in Ross's and lesser snow goose nests examined 2001-2004 at the Karrak Lake goose colony, Nunavut.

Year	# of Plots	# of Nests	Prevalence of Blood (%)	Average Proportion of Egg Covered by Blood (%) (Range)
2001	86	916	74.7	3.04 (0-90)
2002	12	289	97.9	7.41 (0-95)
2003	77	844	55.2	2.86 (0-75)
2004	175	1225	79.9	2.74 (0-70)

Table 2.2. Model selection for variables influencing flea abundance (indicated by average proportion of eggs covered by blood) in Ross's and lesser snow goose nests at the Karrak Lake colony, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, 2001-2004 ($n = 3274$). Only those models with $\Delta\text{AICc} < 2$ are shown, ranked by ascending ΔAICc , 20 candidate models were considered.

Number and Model ^a	AICc ^b	ΔAICc^c	ω_i^d	K ^e
1 {clutchsz bowl plotage habitat year inc}	12661.32	0	0.51	13
2 {clutchsz density species bowl plotage habitat year inc}	12662.63	1.31	0.27	15
3 {clutchsz density bowl plotage habitat year inc}	12662.99	1.67	0.22	14

^a All models considered were for additive effects between factors; factors included clutch size (clutchsz), goose species (species), age of nest bowl (bowl), history of nesting (plotage), nesting habitat (habitat), number of geese on plot (density), and year effects (year). Incubation stage at which the nest was observed (inc) was controlled for in every model.

^b Akaike's Information Criterion with small sample correction.

^c Difference in AICc values between the model with the lowest AICc value.

^d Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).

^e Number of estimable parameters.

Table 2.3. Parameter estimates of proportion of egg covered by blood for variables included in the most parsimonious model (determined with Akaike's information criterion) of factors influencing flea abundance in Ross's and lesser snow goose nests in the Karrak Lake colony, 2001-2004 ($n = 3274$). Estimates derived from general linear model using ESTIMATE option (\pm SE).

Parameter	Estimate (\pm SE)
Clutch Size	0.41 (\pm 0.13)
History of Nesting	0.19 (\pm 0.04)
Bowl Age	
Old	3.77 (\pm 0.72)
New	1.34 (\pm 0.70)
Habitat Type	
Birch	3.02 (\pm 0.80)
Heath	1.77 (\pm 0.72)
Moss	1.87 (\pm 0.69)
Rock	3.85 (\pm 0.83)
Mixed	2.56 (\pm 0.70)
Year	
2001	1.55 (\pm 0.72)
2002	5.62 (\pm 0.80)
2003	1.40 (\pm 0.73)
2004	1.65 (\pm 0.70)

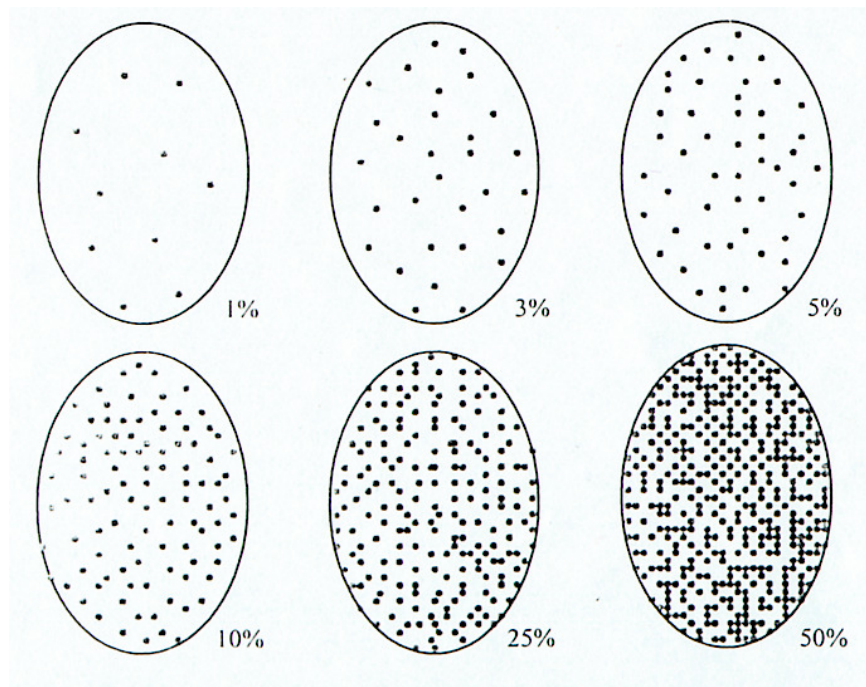


Figure 2.1. Standard aid used to estimate proportion Ross's and lesser snow goose eggs covered by blood from 2003-3004 in the Karrak Lake goose colony, Nunavut.

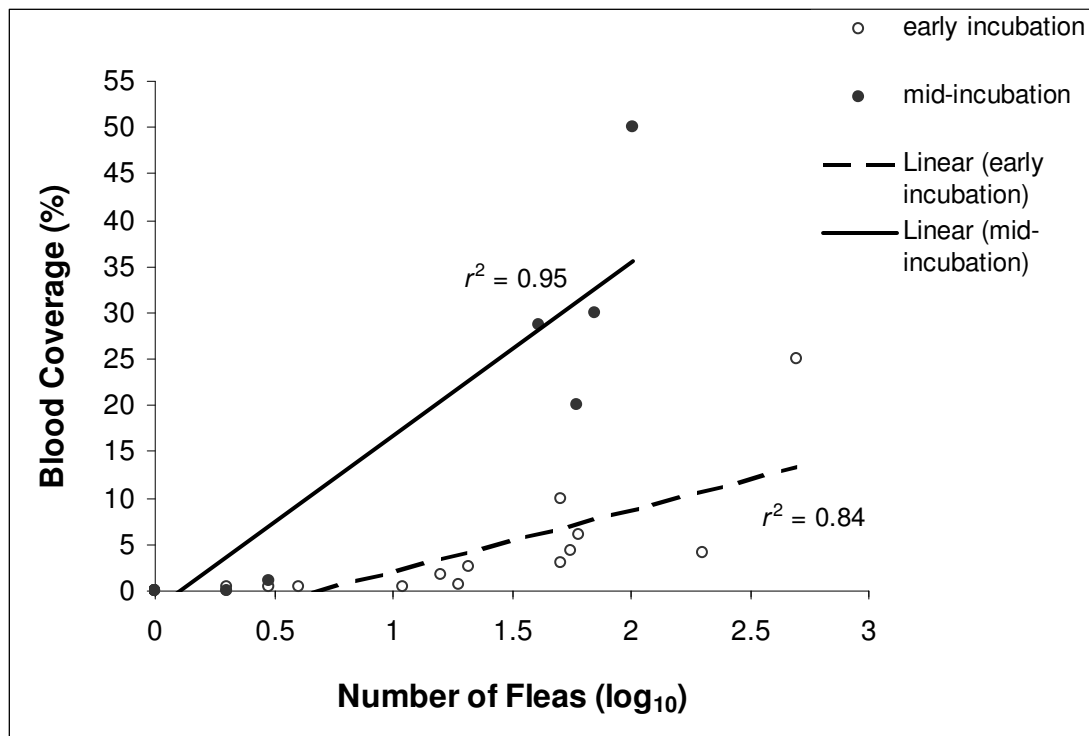


Figure 2.2. Average proportion of eggs covered by blood in relation to number of adult fleas detected in Ross's and lesser snow goose nests collected during early incubation 2004 ($n=15$) and mid-incubation 2003 ($n=11$). Each point $n=1$, except when number of fleas at mid-incubation point zero where $n=5$ and at early incubation point 0.3 where $n=3$. Values of r^2 obtained from analyses, x-axis converted to log to better depict relationship.

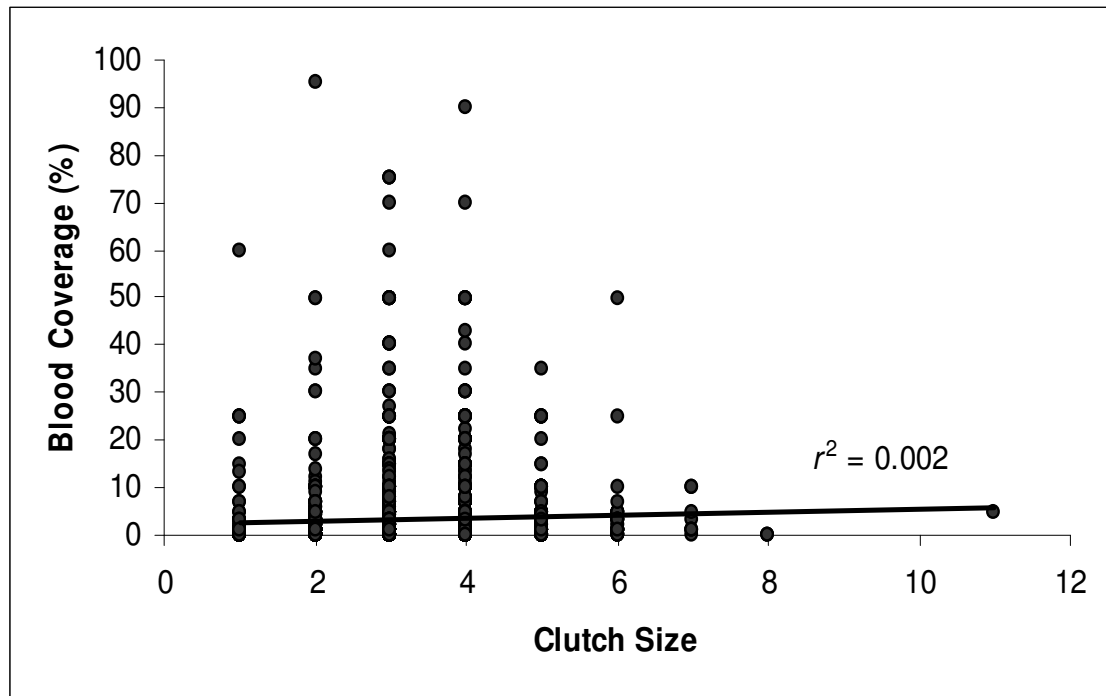


Figure 2.3. Average blood-coverage on eggs in relation to clutch size of Ross's and lesser snow geese 2001-2004 at the Karrak Lake goose colony, Nunavut ($n=3274$).

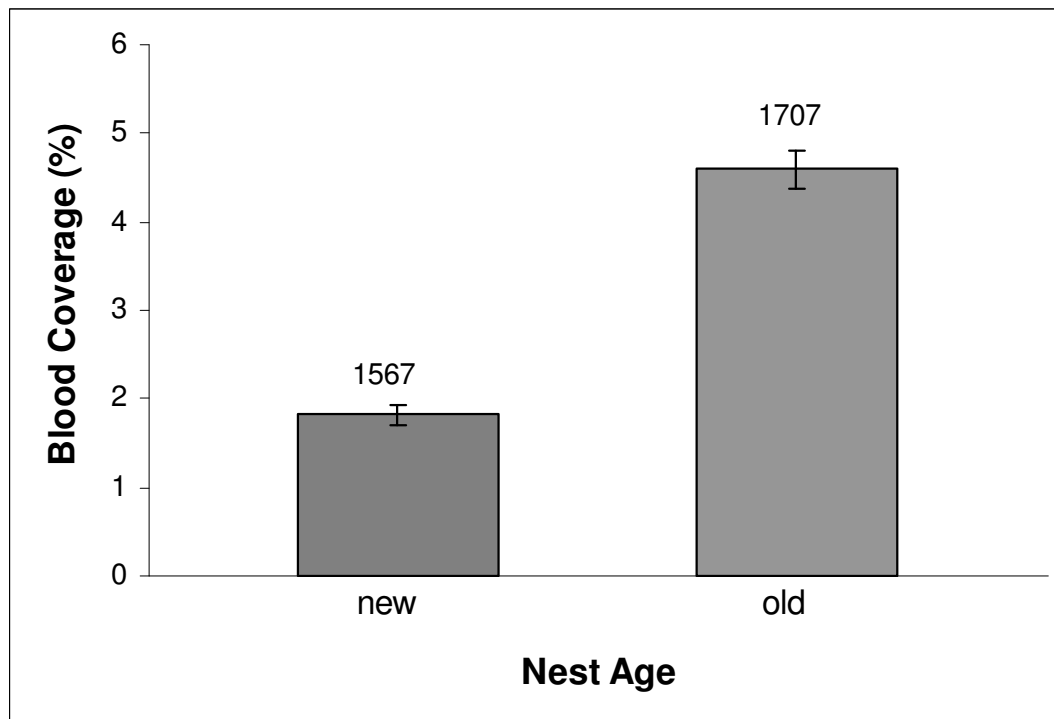


Figure 2.4. Effect of nest age (new vs. old) on average proportion of Ross's and lesser snow goose eggs covered by blood, with 95% C.I. and sample size, from 2001-2004 at the Karrak Lake goose colony, Nunavut.

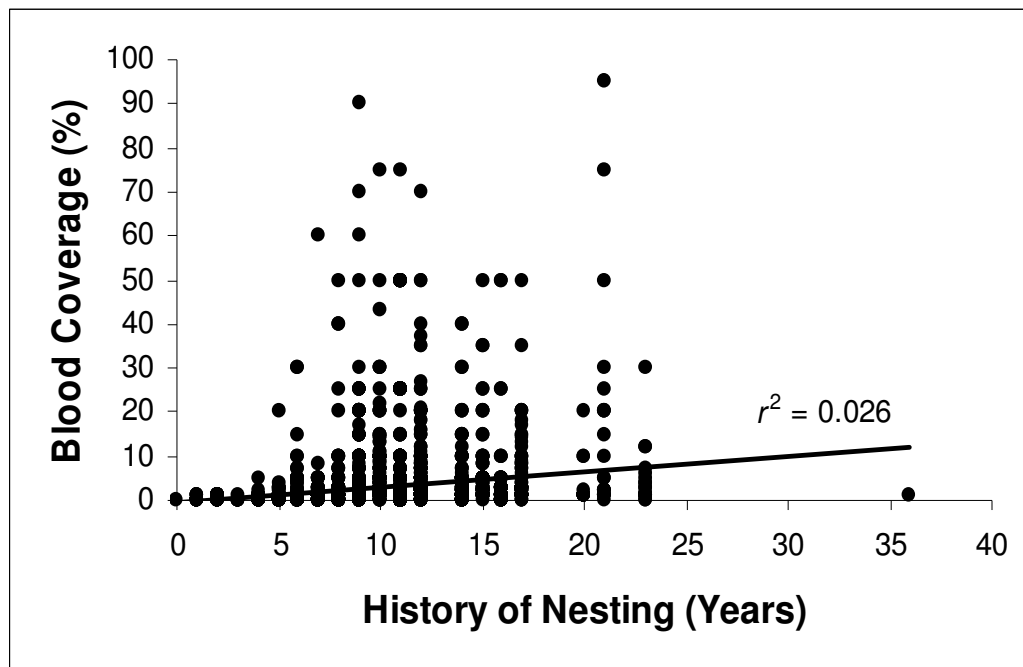


Figure 2.5. Effect of number of years geese had been nesting on a plot on average blood-coverage on Ross's and lesser snow goose eggs from 2001-2004 at the Karrak Lake goose colony, Nunavut ($n=3274$).

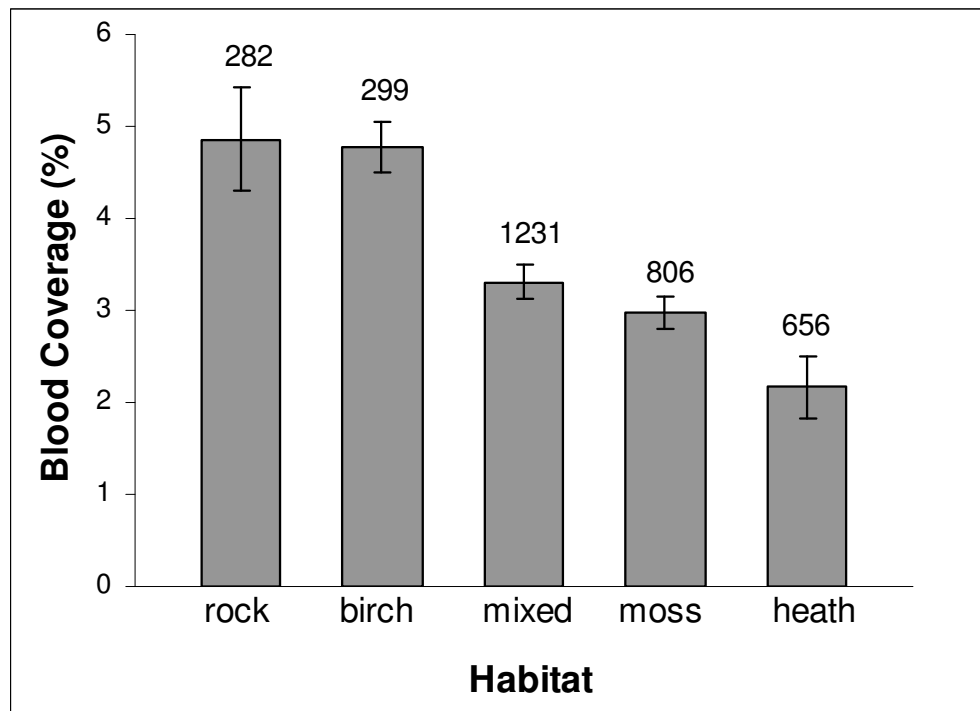


Figure 2.6. Effect of predominant habitat type within 0.5m of Ross's and lesser snow goose nests on average blood-coverage on goose eggs, with 95% C.I. and sample size, 2001-2004 at the Karrak Lake goose colony, Nunavut ($n=3274$).

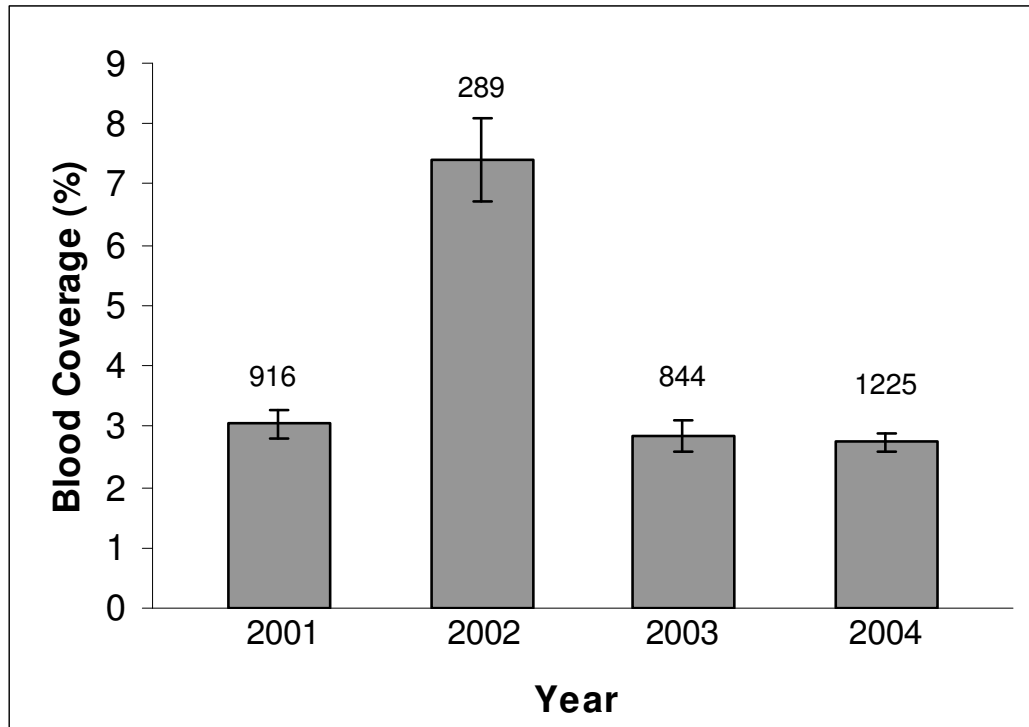


Figure 2.7. Annual variations in average proportion of eggs covered by blood, with 95% C.I. and sample size, on Ross's and lesser snow goose eggs from 2001-2004 at the Karrak Lake goose colony, Nunavut.

CHAPTER 3: OF FLEAS AND GEESE: THE IMPACT OF AN APPARENTLY NEWLY EMERGING DISEASE ON REPRODUCTIVE SUCCESS

3.1 INTRODUCTION

Effects of parasites on their hosts may be more subtle than those imposed by disease agents, and thus more difficult to measure (Begon et al. 1990). Studies aimed at determining the ability of parasites to influence host reproduction have had variable outcomes (Hanssen et al. 2003, Burns et al. 2005). In the past, parasites have been thought to minimize impacts on their host (Tompkins et al. 2001) due to their obligate nature and the presumption of co-evolution between host and parasite; however, recent studies have documented negative impacts on host reproductive success (de Lope et al. 1998, Marzal et al. 2005). Despite requiring a host during only part of their life cycle, ectoparasites may influence the reproductive success, offspring condition, and immune response of their host (Richner et al. 1993, Saino et al. 1999, Thomas and Shutler 2001, Fitze et al. 2004). Most studies of ectoparasitic effects on avian fitness have been focused on passerine species. For instance, hen fleas (*Ceratophyllus gallinae*) and haematophagous mites reduced both nest success, and number of fledglings in great tits, *Parus major* (Richner et al. 1993, Heeb et al. 2000, Fitze et al. 2004). Ectoparasites also induced host behavioral responses in passerines through decreased reproductive investment (O'Brien and Dawson 2005), extension of incubation (Fitze et al. 2004), and

delayed egg laying (Møller 1993). There is a lack of information regarding the effect of ectoparasites on avian species with precocial young, and effects of nest parasites on a waterfowl species or nest parasites in arctic regions have not been reported.

Roughly 90% of the world's population of Ross's geese (*Chen rossii*) and 15% of lesser snow geese (*Chen caerulescens caerulescens*) breed in the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS) in Nunavut, Canada (Drake and Alisauskas unpublished data). The Karrak Lake colony is one of the largest colonies of Ross's and lesser snow geese known in the QMGMBS (Alisauskas et al. 1998). Blood-covered eggs were detected in goose nests in the Karrak Lake colony in 1991, and in 1997 it was noted that ectoparasites were associated with these nests. However, other causes of blood-covered eggs had not been excluded. Not only had the prevalence of blood-covered eggs in the colony increased since first noted in 1991, but the entire surface of some eggs were covered with dried blood. The ectoparasites were subsequently identified as the flea *Ceratophyllus vagabundus vagabundus* (Boheman 1866), which had not previously been reported in association with Ross's or snow geese (Harriman et al. unpublished data).

Bird fleas spend most of their life in their host's nest, as egg, larval, and pupal development usually occur off of the host (Marshall 1981). Adult fleas in northern climates emerge with host arrival (Askew 1971). Larvae are rarely parasitic (Boyd 1951), primarily feeding on undigested blood defecated by adult fleas, and to a lesser extent, on nest cup material (Marshall 1981). The blood on goose eggs likely results from feeding by adult fleas on incubating female geese, with subsequent defecation on goose eggs.

The populations of Ross's and snow geese have been growing at unprecedented high rates. Parasite and host populations often cycle together in an ecosystem. In general, populations are believed to be regulated by density-dependent factors (Begon et al. 1990). In cases where populations have been released from previously regulating factors, new limiting factors can arise as stressors which begin to limit and depress host population growth. Ectoparasites may play a role in regulating goose populations. Parasites are presented with a predictable host source in established, long-term colonies. The close proximity and behavior of animals in colonies provide an ideal environment for parasite persistence, and parasite impacts may be magnified on colonial-nesting birds due to an increased likelihood of disease transmission (Alexander 1974).

I assessed interactions between fleas and Ross's and lesser snow geese in the Karrak Lake goose colony from 2001-2004 as part of a long-term study in this colony. The objective was to test the hypothesis that parasite abundance, determined by proportion of eggshells covered by blood, had a detrimental effect on goose reproduction. I was interested primarily in whether or not parasites influenced nest success, but modeled the effect of other ecological covariates also thought to play a role in goose nest success.

3.2 METHODS

3.2.1 Study Area

This study was conducted at the Karrak Lake goose colony (67°14'N, 100°15'W), located ~60 km south of Queen Maud Gulf, Nunavut, in the QMGMB. The colony covers about 360 km², of which 200 km² is terrestrial habitat. Geese arrive in the colony

in late May and depart in early July, after a 23 day incubation period. Goslings are precocial, leaving the nest soon after hatching. During 2001-2004, annual nest density averaged 22-34 nests/ha with a range of 0-250 nests/ha (Alisauskas unpublished data).

3.2.2 Fleas in the Karrak Lake Colony

The flea, *C. v. vagabundus*, over-winters in goose nests as a pupa in a cocoon. Fleas hatch the next spring probably in response to increased temperatures and vibrations (Marshall 1981), such as when geese disrupt an area during nest construction and egg laying. It appears that there is only one period of adult flea emergence during the period of goose nesting. Blood is deposited by fleas on goose eggs within the first few days of incubation by geese and continues to be deposited until ~4 days into incubation. Absence of new blood there after likely indicates the cessation of mobility in response to being gravid, or death of adult fleas.

The amount of dried blood on eggs is slowly reduced as geese roll and rearrange eggs in nests during incubation (Harriman et al. unpublished data). A greater proportion of blood persists at the poles of the eggs than on the middle, presumably because of less abrasion at the poles. In heavily infested nests, female geese may never completely remove blood from egg surfaces for the duration of incubation, thus the pole of eggs in some nests often retain dried blood throughout the nesting period.

3.2.3 Experimental Design

Data for this study were collected from nest plots from 2001-2004. Nest plots have been used continuously since 1993 to monitor variation in nest initiation date, clutch size, hatch date, and nest success of geese, and to determine species composition and population size of the colony. Plots were placed systematically throughout the colony on a 1 km by 1 km grid and marked with a center pole. Nest plot data were collected by many different individuals each year (up to 20 people/year). Every nest within a 30 meter radius around the center marker was recorded, and the distance to each nest from the center of the plot was measured. Early in incubation, each nest was numbered, and each egg was marked with the nest number and the egg number. The length and width stage of each egg were recorded. Goose species was determined from egg measurements following Alisauskas et al. (1998). Egg candling (Weller 1956) was used to determine the incubation stage of eggs in each nest. Use of nest bowls from previous years was determined by the presence of egg membranes, old down, or old nest markers. The dominant habitat type within 0.5m of each nest was also recorded. Habitat was classified as rock, mixed (gravel-filled soil upon which low vascular plants grow sparsely), heath, birch, or moss. Plots were visited once during incubation. Each nest was re-visited after geese and goslings left the colony. A nest was considered successful if at least one egg hatched, determined by the presence of gosling down, egg cap, and/or egg membrane. Nest density was number of nests initiated/plot, regardless of status (failed, etc.). The history of nesting occupancy at individual plots was calculated using data from 1966-2004 (Kerbes 1994, Alisauskas et al. 2006). The first year at least one

bird was observed nesting in a plot was subtracted from year of data collection to determine number of years of nesting at each plot.

Fleas deposited blood on goose eggs, and the amount of blood was directly correlated with number of fleas counted/nest (Chapter 2). Therefore, as an index to adult flea abundance, the proportion of each eggshell covered by blood in a nest was visually estimated; this would aid in determining whether there was a relationship between flea abundance and goose nest success. The proportion of blood on eggs was recorded with the aid of a visual reference to improve consistency among observers in 2003-04, but not in 2001-02, and was averaged over the entire nest visually. The proportion of blood appeared to be consistent among eggs of the same nest regardless of laying order, or variation in egg size.

3.2.4 Analyses

A logistic regression was used to determine how nest fate varied in relation to coverage of egg surface by blood, species, nest density, habitat type, nest initiation date, age of nest bowl, history of nesting on plot, clutch size, and year. Specifically, the aim was to determine whether or not flea abundance (as indicated by the degree of blood-coverage on eggs) was an important influence on nest success. The incubation stage of each clutch was controlled for in every model, as plots were observed throughout incubation and we were aware that blood rubbed off of eggs as incubation progressed. Density of birds and nest initiation date were positively correlated, and therefore these variables were not included in the same model. No other variables were closely correlated. Eighty *a priori* candidate models were considered. Only additive models were

considered because of uncertainty of ecological relevance of interactions among covariates.

Akaike's information criterion adjusted for small sample size and number of parameters (AICc) was used to rank quality of models about variation in nest fate (Burnham and Anderson 2002). Values for AICc, differences in AICc from the best model ($\Delta AICc$), and model weights (w_i) were calculated using AIC from PROC LOGISTIC (SAS Institute Inc., 2001). Additionally, I used all data collected from 2001-2004 which contained blood coverage and nest success to report patterns between these variables among years.

3.3 RESULTS

Number of plots and nests examined, prevalence of nests containing blood-covered eggs in colony, average coverage of blood, and goose nest success for the 4 years of the study are shown in Table 3.1. The top five models all included blood percent, year, clutch size, and species. The best model suggested that blood coverage, species, nest initiation date, history of nesting, clutch size, and year were all important factors in determining nest fate ($\chi^2=253.72$ df=9, $P<0.001$, Table 3.2). Nest success varied by goose species ($\chi^2=29.33$, df=1, $P<0.001$) with Ross's goose nest success being higher during two years and both goose species experiencing similar success rates during two years. Clutch size influenced nest success ($\chi^2=31.59$, df=1, $P<0.001$), with nests containing 3 and 4 egg clutches experiencing the highest success. Nest success varied annually ($\chi^2=134.25$, df=3, $P<0.001$; Table 3.1). Nest initiation date ($\chi^2=3.33$, df=1, $P=0.07$) and history of nesting ($\chi^2=2.51$, df=1, $P=0.11$) did not significantly influence nest success.

The average amount of blood on eggs influenced nest success ($\chi^2=30.16$, $df=1$, $P<0.001$). There appeared to be a threshold in coverage of eggs by blood, beyond which nest success decreased, and this threshold varied annually; in 2001 and 2003, this threshold was reached when the coverage of eggs by blood reached >20% (Figure 3.1). In 2004, nest success was reduced when coverage of eggs by blood averaged >5%. Accordingly, the proportion of the colony negatively influenced by blood-coverage varied annually, ranging between 0-13% (Figure 3.2).

3.4 DISCUSSION

3.4.1 Impact of Flea Abundance on Nest Success

Despite the relatively short lifespan of adult *C. v. vagabundus*, the top five models suggested that blood on goose eggs, resulting from feeding by adult fleas on nesting geese, negatively influenced hatching success of goose nests. There are at least three possible explanations for why nest success decreased with increased flea abundance: 1) alterations in female goose behavior 2) decrease in gas exchange across eggshell membranes and 3) increased predator attraction due to blood scent.

Fleas may have affected goose behavior. Some species of birds avoid or desert nests infested by ectoparasites (Duffy 1983, Moore 2002, Fitze et al. 2004). Presence of haematophagous insects can be energetically costly by inducing annoyance reactions from their hosts (Toupin et al. 1996, Hagemoen and Reimers 2002). Females incubating nests with high parasite abundance may experience irritation from biting fleas, and so reduce attendance at nests. Discomfort of geese from fleas may increase the goose's frequency and/or duration of breaks from incubation, which may in turn negatively

affect nest success through cold-induced embryo death or higher likelihood of predation during parental absence (Samelius and Alisauskas 2000, 2001). Fleas increased parental effort through the extension of incubation duration in a passerine (Fitze et al. 2004). The extension of incubation may increase nest abandonment and likelihood of predation.

Another explanation for nest failure, unrelated to host nest attendance, is that blood on the surface of goose eggs may have a direct effect through impedance of gas exchange. All requirements of embryonic development are met with material supplied by contents of avian eggs, except for oxygen. Eggshells contain pores through which developing embryos obtain oxygen. Avian eggs contain two membranes inside the eggshell (Romanoff and Romanoff 1949). An air cell forms between these membranes at one pole of the egg (Ar and Rahn 1980). Rokitka and Rahn (1987) found that the density of eggshell pores is greatest on the pole in which the air cell is formed, with lower pore density along the sides of eggs, and lowest density at the more pointed pole. Oxygen exchange and consumption are greatest in the polar region of the egg containing the air cell (Seymour and Visschedijk 1988).

Effective gas exchange is likely to be reduced through pores plugged or covered by dried blood. Rodricks et al. (2004) wrapped chicken eggs with an impermeable film, longitudinally covering 50% of the eggshell surface. Eggs wrapped 14-18 days into incubation had decreased hatching success and produced chicks with memory deficits. Unlike the study by Rodricks et al. (2004), presumed blockage of pores by dried blood in our study was not limited to half of the egg, but disproportionate coverage occurred at the poles. This may explain why there was a threshold in the proportion of the egg's surface covered by blood above which nest success declined, but appeared unaffected below that threshold. Eggs with greater coverage by blood retained blood on the poles

longer into incubation. This could be especially detrimental to developing goose embryos due to the importance of the air cell pole for gas exchange.

Finally, the scent of blood on eggs may have attracted mammalian nest predators, particularly arctic foxes (*Alopex lagopus*), much more than nests that contained eggs without blood. Although geese present at nests most often deter or repel foraging foxes, increased contact between foxes and nests undoubtedly increases probability of egg loss (Samelius and Alisauskas 2001).

3.4.2 Annual Variation in Impact of Flea Abundance

During most years adult flea abundance negatively impacted nest success. In 2002 nest success was not significantly influenced by flea intensities. Small sample size may have influenced the outcome during this year. In 2004, nest success decreased for those nests with >5% coverage of eggs by blood, unlike 2001 and 2003 in which only nests with >20% blood experiences a decrease in nest success. This difference may have been due partly to extreme weather conditions during the nesting period in 2004. Female energy shortages may be more common in inclement weather (Williams 1996). Mean ambient temperature in 2004 was near the long-term average during nesting, but precipitation was greater than normal. In 2004, there was an average 1.6 mm (55%) more precipitation/day than in any of the three previous years. Flea abundance may have greater impacts on geese during years of abnormal conditions, as fleas can increase nestling mortality disproportionately during cold, rainy conditions (Merino and Potti 1996).

Incubating female geese may alter their behavior during years of abnormal precipitation. Two of the three hypotheses pertaining to how fleas influence nest success, decrease in parental attendance and impedance of gas exchange, are consistent with this prediction. The influence of annoyance by fleas on reduced incubation constancy may be amplified in years with abnormal weather conditions. Inclement weather decreases female body condition regardless of parasite abundance (Jones 1987). Poor weather conditions, and hence decreased female body condition, in conjunction with flea-induced annoyance may increase rates of nest desertion. Conversely, altered female behavior in the face of extreme environmental conditions might increase effects of blood on gas exchange through eggshells. Adverse weather conditions increase nest attentiveness (Skutch 1962). Although geese might have increased nest attentiveness, they might have lessened energy expenditure via decreased egg manipulation. Reduced frequency of egg rotation by nesting females may result in slower removal of blood from eggs.

It seems unlikely that the hypothesis indicating increased predation in response to the scent of blood-covered eggs alone could explain annual variations in the impact of fleas on goose nest success. The preferred food source of arctic foxes at Karrak Lake is collared lemmings (*Dicrostonyx torquatus*). The abundance of collared lemmings in 2004 was similar to that in 2002 and 2003. Additionally, of the years of study, fox numbers in the colony were at their lowest in 2004 (Samelius 2006). Reduced nest attendance by incubating geese is known to be linked to increased likelihood of egg predation by arctic foxes (Samelius and Alisauskas 2001). So, alterations in behavior by incubating geese and their mates, such as longer or more frequent breaks potentially in response to flea abundance, could have increased the loss of eggs to foraging foxes, and

so reduced egg success and nest success. Although predation might play a role in failure of nests containing blood-covered eggs, female behavior in response to fleas would likely be the ultimate cause of nest failure.

3.4.3 Flea Impacts on Karrak Lake Goose Population

Although nest success of individual geese was apparently influenced by fleas it is important to consider the potential population level effects of fleas on geese nesting in the Karrak Lake colony. During years of reduced nest success of nests with >20% blood coverage, 4-6% of the birds in the colony potentially experienced significantly lower nest success. In 2004, when any level > 5% blood coverage was associated with decreased nest success, over 13% of the population was potentially influenced (Figure 3.2).

Parasites often are clumped due to host location and density. In addition, individuals of these aggregated parasites are further clumped: a few individuals may host many parasites, while most individuals have few or no parasites (Crofton 1971, Anderson and May 1978, Poulin 1993). Diseases regularly grow explosively (Akçakaya et al. 1999). However, the aggregation behavior of parasites may reduce the possibility of wide-spread decline of the host population (Begon et al. 1990). Stable regulation of the host population is likely to occur when many ectoparasites are present in few individuals (Tompkins et al. 2001). However, it is possible that parasite abundance and/or distribution may change.

Growth by colonial populations of Ross's and snow geese has resulted in large-scale alteration of vegetation communities at Karrak Lake through grazing and nest

construction (Alisauskas et al. 2006). Goose grazing has caused long-term changes to vegetation on their breeding grounds elsewhere in the arctic (Kerbes et al. 1990, Ganter et al. 1996, Jano et al. 1998). Although most geese remain in colonies that have undergone intense shifts of plant species, new recruits often settle in the less disturbed peripheral habitat (Ganter and Cooke 1998). This behavior causes an increase in area that is negatively affected by breeding geese. Parasites are able to respond to the external environment in the absence of their host. Strategies of virulence and how many offspring to produce depend somewhat on host reaction to environmental variation (Thomas et al. 2002). An increase in flea range in the colony could increase flea persistence in years in which entire areas are either not used by geese or in which goose nests fail due to a natural event. Consistent growth in goose numbers and the increase in breeding area provide parasites with an abundance of hosts and increase the likelihood of parasite population stability.

Fleas may become a limiting factor for geese nesting at Karrak Lake if flea intensities climb. Knowledge of factors that influence rates of flea abundance in this colony may assist researchers in making predictions about the spread of this disease. Particularly, host colony size is likely a factor that influences ectoparasite abundance. Numbers of ectoparasites per nestling and per nest were positively correlated with size of host colonies in bank swallows (*Riparia riparia*; see Hoogland and Sherman 1976) and cliff swallows (*Hirundo pyrrhonota*; see Brown and Brown 1986). High densities of ectoparasites can increase rates of nestling dispersal and adult desertion (Duffy 1983, Brown and Brown 1992, 1992, Fitze et al. 2004). Dispersing birds often breed in smaller colonies the following year (Fitze et al. 2004). Birds in smaller colonies are susceptible to higher predation rates (Raveling 1989). Geese that disperse to smaller

newer colonies with fewer parasites may face a trade-off of reduced likelihood of ectoparasite infection but at the expense of increased likelihood of predation.

In 1998, there were 73 active goose colonies known in the QMGMBs (Kerbes et al. 2006). However, about 90% of all nesting Ross's and lesser snow geese in the sanctuary are found in four large and persistent colonies. Smaller colonies in the QMGMBs tend to be less permanent. Less persistent colonies are less likely to have fleas because of inconsistent presence of goose hosts. Therefore, we would expect the flea population at highest densities in older, larger colonies that harbor geese without interruption each year. Within the last 5 years, the presence of blood has been noted in an equally large and more rapidly growing colony in the QMGMBs, located ~100 km NNE of Karrak Lake. In addition, researchers at the McConnell River colony, which is located on the west coast of Hudson Bay and primarily composed of Ross's geese, have noted blood on eggs during the last 3 years (Caswell and Baldwin personal comm.). Although abundance of fleas in the McConnell River colony appears to be lower than that seen in the QMGMBs, it is indicative that fleas are apparently establishing themselves in goose colonies in other parts of arctic Canada and may be more prevalent geographically than was previously thought.

The objective was to determine whether the abundance of flea ectoparasites, determined by egg blood-coverage, influenced Ross's and lesser snow goose reproductive success. I conclude that flea abundance inversely affected goose nest success in most years. The magnitude of this effect varied annually. The mechanisms behind these results remain unclear, although I suspect that either or both female behavior and impedance of gas exchange through eggshells likely contributed to nest failure in infested nests. Annual variation in the influence of flea abundance on goose

nest success may be partly attributed to weather conditions. Some global warming models predict increased precipitation and temperatures in the arctic (Rouse et al. 1997). My data suggest that geese may be more susceptible to parasites when high precipitation rates occur during nesting. Additionally, increased temperatures may reduce existing constraints on parasite survival in northern climates. These climatic changes may allow for larger effects on host populations.

Table 3.1. Number of plots and nests observed, prevalence of nests containing blood-covered eggs, average egg blood-coverage, and nest success of Ross's and lesser snow geese examined 2001-2004 at the Karrak Lake goose colony, Nunavut.

Year	# of Plots	# of Nests	Prevalence of Blood (%)	Average Percent of Egg Covered by Blood (Range)	Overall Nest Success (%)
2001	86	916	74.7	3.04 (0-90)	68.6
2002	12	289	97.9	7.41 (0-95)	86.9
2003	77	844	55.2	2.86 (0-75)	87.8
2004	175	1225	79.9	2.74 (0-70)	70.6

Table 3.2. Model selection for variables influencing nest fate on Ross's and lesser snow geese (averaged per nest) at the Karrak Lake colony, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, 2001-2004 ($n = 3274$). Only those models with $\Delta\text{AICc} < 2$ are shown, ranked by ascending ΔAICc , 80 candidate models were considered.

Number and Model ^a	AICc ^b	ΔAICc^c	ω_i^d	K ^e
1 {bloodmn year clutchsz species nidjul plotage inc}	3343.57	0	0.21	11
2 {bloodmn year clutchsz species nidjul inc}	3344.26	0.84	0.15	10
3 {bloodmn year clutchsz species plotage inc}	3344.66	1.08	0.12	10
4 {bloodmn year clutchsz species nidjul bowl plotage inc}	3344.97	1.39	0.11	12
5 {bloodmn year clutchsz species nidjul bowl inc}	3345.20	1.63	0.09	11

^a All models considered were additive effects between factors; factors included average percent of blood on eggs per nest (bloodmn), year effects (year), clutch size (clutchsz), goose species (species), age of nest bowl (bowl), history of nesting (plotage), and nest initiation date (nidjul). Incubation stage at which the nest was observed (inc) was controlled for in every model.

^b Akaike's Information Criterion with small sample correction.

^c Difference in AICc values between the model with the lowest AICc value.

^d Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).

^e Number of estimable parameters.

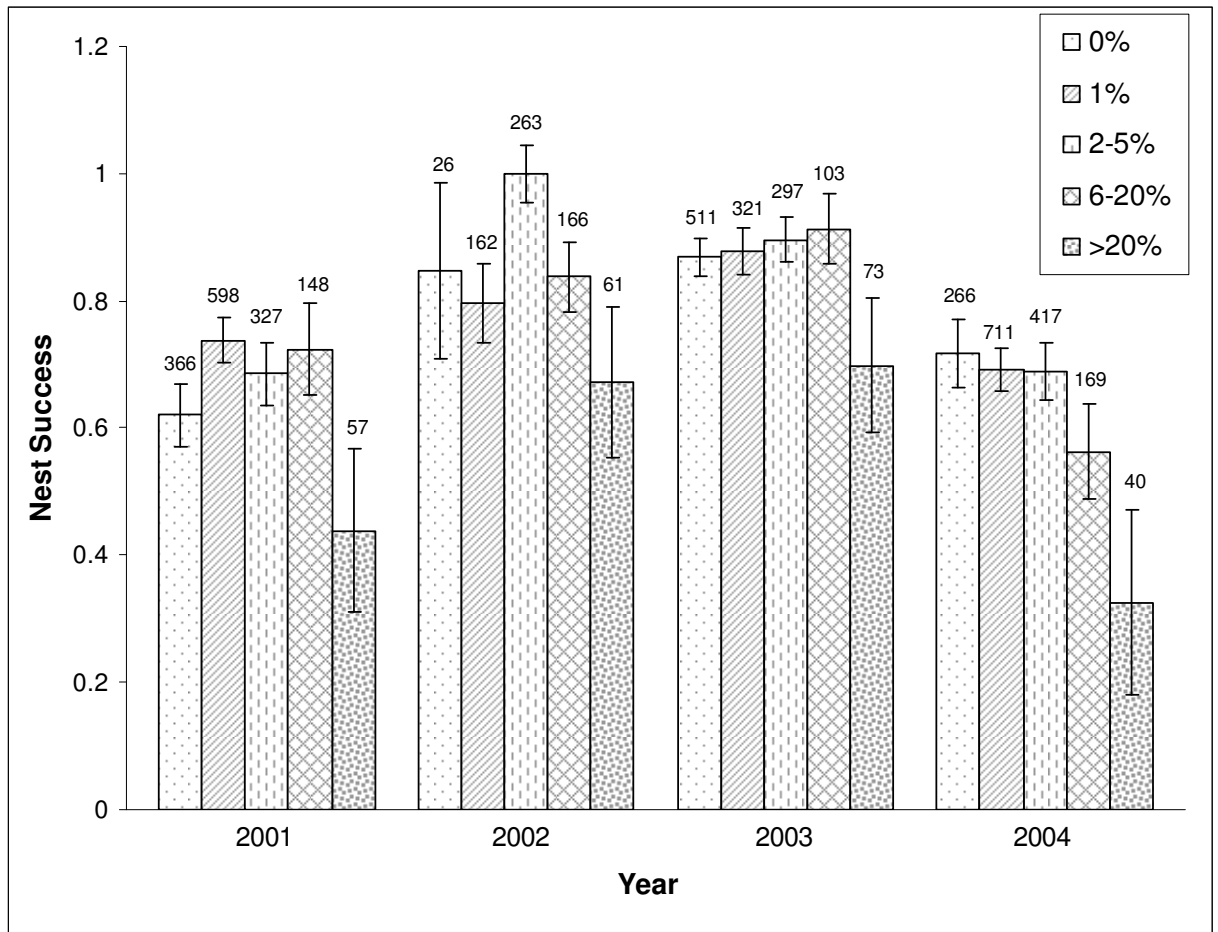


Figure 3.1. Mean (\pm SE) annual nest success of Ross's and lesser snow geese stratified by extent of coverage of eggs with blood (number of nests sampled reported above error bar). Blood on eggs results from feeding on host geese by fleas at Karrak Lake, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, 2001-2004.

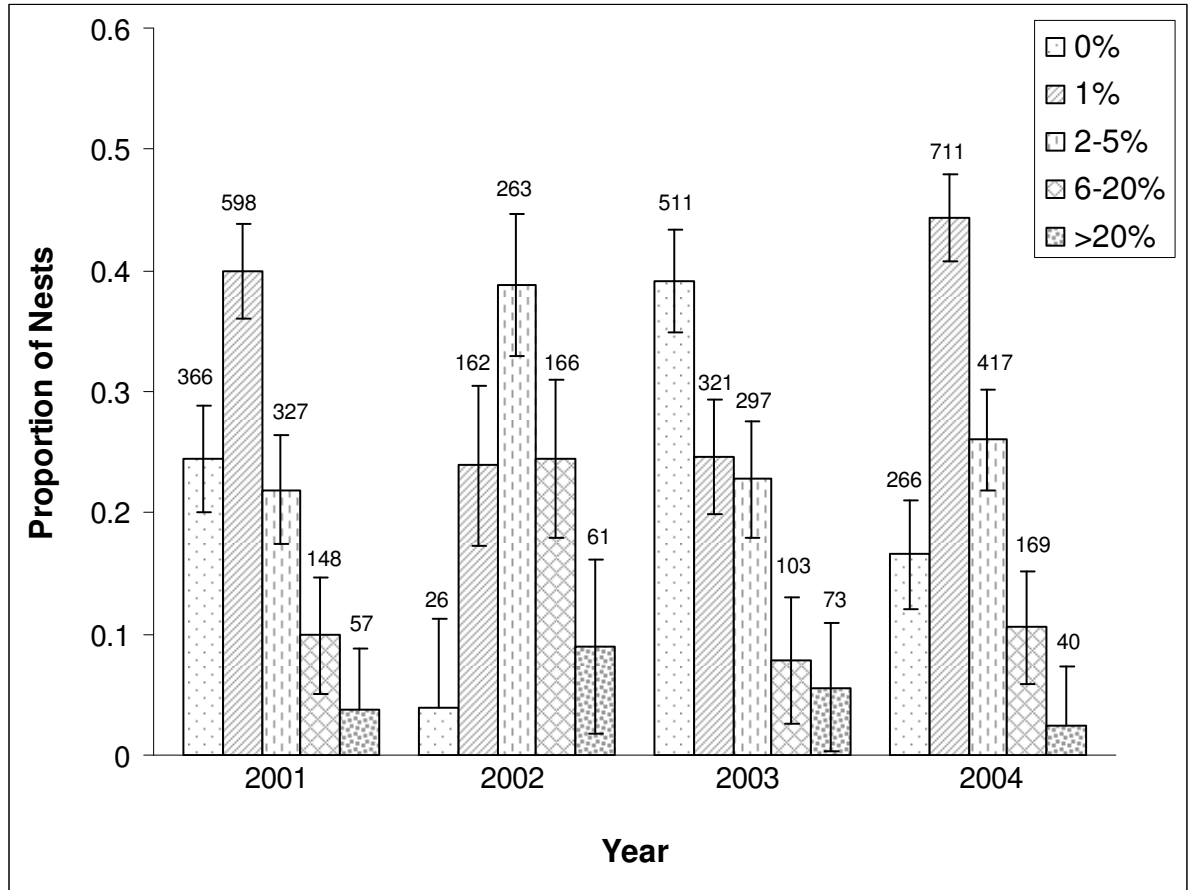


Figure 3.2. Mean (\pm SE) proportion of Ross's and lesser snow goose nests stratified by extent of coverage of eggs by blood by year (number of nests sampled reported above error bar). Blood on eggs results from feeding on host geese by fleas at Karrak Lake, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, 2001-2004.

CHAPTER 4: SUMMARY AND SYNTHESIS

Studies of impacts on avian reproductive success by ectoparasites have been primarily focused on species with altricial young (Richner et al. 1993, Saino et al. 2002, Fitze et al. 2004). I investigated correlates of flea (*Ceratophyllus vagabundus vagabundus*) abundance in nests of colonial-nesting arctic geese (*Chen rossii* and *Chen caerulescens caerulescens*), and the impacts of flea abundance on reproductive success of host geese. Herein, I summarize my most significant findings and discuss the implications of these findings.

To my knowledge, my work was the first study on nest parasites of an arctic-nesting species, on nest parasites of waterfowl, and of birds with precocial young more generally. Blood has never been reported on eggs to the extent observed in the goose colony at Karrak Lake. Between 60 and 95 percent of geese in the colony were infested with at least one flea during 2001-2004. Confirming a relationship between blood-coverage on eggs and flea abundance was essential for this study. The first part of chapter 2 addressed this relationship using bird and nest collections. Flea numbers in nests were positively correlated with blood-coverage on eggs of the corresponding nest in both years, but flea intensities on birds did not correspond to blood-coverage on eggs both years. Bird fleas spend most time in their host's nest (Marshall 1981), so this outcome was consistent with expectations (Rothschild and Clay 1952). Coverage of eggs by dried blood was a good correlate of flea abundance in nests and so was used as an index of flea abundance in individual nests for the remainder of the thesis.

In chapter 2, I also examined flea abundance in relation to individual host attributes such as species (Ross's goose vs. lesser snow goose), clutch size, and nest initiation date but also in relation to the host's environment, including age of nest bowl, history of nesting by geese on a specific plot within the colony, nesting habitat, and nest density. Although flea abundance differed with variations in clutch size and habitat that geese nested in, it appeared that the most important factors influencing flea abundance were age of nest bowl, history of nesting on plot, and year of study.

Flea intensities varied throughout the colony, and chapter 3 addressed the impact of varying flea intensities on goose nest success. Many factors are known to influence goose reproductive success. In general, increased goose nest success is associated with earlier arrival on the breeding ground (Bêty et al. 2004), an increase in alternative prey species of arctic foxes (*Alopex lagopus*; Bêty et al. 2001), lower nest density (Bêty et al. 2001), younger geese (Rockwell et al. 1993), and nesting habitat quality (Jackson et al. 1988); weather also plays an important role, as increased nest success is also related to reduced precipitation and higher ambient temperatures from the time of arrival by nesting adults in May or early June until their young hatch in July (Skinner et al. 1998). I was interested specifically in the role that adult fleas had on nest success over and above previously described influences. I found that blood-coverage was an important negative influence on nest success in most years, but that the effect of fleas varied annually. In two years, nest success declined only when blood-coverage was >20%. However, nest success in 2004 declined when blood-coverage was >5%. In that year, 13% of geese in the colony were estimated to have experienced significantly lower nest success in response to flea abundance. The mechanism behind reduced nest success in response to blood coverage remains uncertain. However, three general hypotheses

invoke 1) alterations in female behavior 2) decrease in gas exchange across eggshell membranes and 3) increased predator attraction due to blood scent.

Evolutionary ecology predicts that organisms make decisions to maximize their fitness (Lomnicki 1988). Birds tend to select for parasite-free nest and roost sites (Brown and Brown 1986, Christie et al. 1994). Such processes for anti-parasite nest selection likely are achieved by species nesting in habitats in which they are able to visually assess nest parasite loads or by individuals that nested in or hatched in the area being avoided (Brown and Brown 1986, Møller 1990). However, geese in the Karrak Lake colony continued to use old nest bowls and they continued to nest in the central, or oldest, areas of the colony. As elsewhere (Brown and Brown 1986), geese in the oldest parts of the Karrak Lake colony were at greater risk of heavier ectoparasite loads than those in newer parts of the colony. The oldest part of the colony is also toward the center, and nests farthest from the colony edge theoretically should be at lower risk of predation (Begon et al. 1990). Thus, such opposing evolutionary pressures may create optimal fitness, through the highest reproductive success, somewhere between the core and edge of the colony.

If fleas are negatively impacting goose nest success during most years then why don't we see geese responding to fleas in the Karrak Lake colony? It may be that fleas are newly emerging, as hypothesized, and geese have therefore yet to evolve in response to their presence. In the absence of fleas, it is likely an adaptive strategy for geese to re-use old nest bowls, therefore possibly saving time and energy by doing so. In the presence of fleas, it is likely adaptive to build new nests and thereby decrease the probability of flea infestation. However, it may be that the benefits of nesting in areas of higher flea abundance, such as a decreased probability of predation or decreased energy

output required to build a new nest, out-weigh the costs. Although fleas may potentially influence goose reproductive success, they failed to do so in one of the four years, and likely impacted only a small proportion of the colony in two other years. The level to which fleas affect geese may not be sufficient enough to induce behavioral change by geese.

Although geese may be able to visually assess parasite loads before nesting in an area, the data suggest that high parasite abundance does not necessarily indicate that goose reproductive success will be impacted. Parasite abundance was highest in 2002, the same year goose nest success was not influenced by fleas. Snow accumulation was deepest 2002 and second deepest in 2004; 2004 was also when the flea's impact on nest success was strongest. Deeper snow may have contributed to an increase in flea overwintering survival. Geese may be able to predict flea population fluctuations upon arrival due to snow depth and could likely avoid older areas of the colony during these years. However, it appears as though unpredictable weather conditions during nesting is what ultimately determines whether flea populations will influence goose nest success. The high amount of precipitation during the nesting season of 2004 may have contributed to apparently increased sensitivity by geese to flea intensities during this year. Weather conditions may have also influenced why this was not the trend in 2002 when flea intensities were highest and precipitation was average. The daily temperatures during the nesting season of 2002 were much warmer, being on average 6°C warmer than 2001, 5°C warmer than 2003, and 3°C warmer than 2004. Temperature and precipitation during nesting may influence the impact of fleas on nest success in any given year.

Hypothesized trends for an increase in temperature and precipitation in the arctic may impact the flea population at the Karrak Lake goose colony. Global warming has already begun to increase parasite populations in the arctic, namely by increasing the length of time parasites have to develop and by expanding the northern boundaries of their ranges (Kutz et al. 2004, Jenkins et al. 2006). Additionally, predictions are that global warming will lead to an increase in the range and density of dwarf birch across the tundra (Sturm et al. 2001). Nests in birch habitat at Karrak Lake showed the highest likelihood of flea abundance, so such predicted increases in birch, in the absence of any behavioral shifts in nest site selection by geese, may enhance ectoparasite prevalence among nesting geese to the detriment of at least their nest success, and possibly to their population growth rate. However, as noted above, increased temperatures during nesting may also contribute to why geese did not experience decreased reproductive success in response to fleas in 2002. An increase in precipitation may enhance the effect of fleas on geese in the Karrak Lake colony. During the 2002 nesting season precipitation was not above average. Although it is likely that the flea population will grow in response to rising temperatures, it remains unclear what the effect on geese will be if rising temperatures are paired with increased precipitation.

More research is needed in order to understand the biology and population dynamics of *C. v. vagabundus* at Karrak Lake and the flea's effects on its host goose population. Host regulation by parasites can be demonstrated by an increase in host density in response to removing a parasite from a population (Tompkins et al. 2001). I aimed to test the hypothesis that fleas regulated goose populations using an experimental approach. In 2004, 10 control and 10 experimental plots were utilized within older areas of the colony. Previously established plots were used as control plots, 100m from which

the center of the corresponding experimental plot was established. Plot locations were selected for the high presence of blood-covered eggs in the previous year and were dominated by rock or birch nesting habitat. Nests in these plots were treated in the same manner as all plots were in previous chapters, with the exception of nests in experimental plots, from which eggs were removed and the entire nest was sprayed with 20ml of 2% permethrin, a commonly used insecticide. It was hypothesized that permethrin would kill emerging fleas and therefore the mean blood coverage would be less and nest success higher in those nests treated with permethrin. If removal of parasites increased nest success (i.e. future goose densities), this experiment may have provided evidence that fleas may aid in regulating goose populations.

No difference in the reproductive success of geese was detected between treated and untreated plots. Also, mean blood coverage did not differ between treated and untreated plots. In retrospect, this may have been due to incorrect execution of the experiment. In 2004, heavy precipitation during the beginning of nesting likely caused goose nest initiation dates to be more variable than normal. Nests were not sprayed until many of the geese had begun nesting, and due to the quick lifecycle of the flea, effects on the geese and their eggs, via annoyance and blood deposition, had already taken place. In order to determine whether goose populations may actually be influenced by fleas, this experiment would have to be repeated over several years and spraying would have to take place multiple times prior to and during nest initiation to ensure that all fleas were killed on the plot before nesting began. Also, nests in control plots should be sprayed with water to control for any effect a wet substance would have on egg hatchability in this often cool climate.

It would be useful to determine the mechanism behind nest failure in response to flea intensities. There are a few ways that this might be approached. An easy and cost effective method would be artificial incubation of eggs with varying blood-coverage. This would control for female behavior, as the incubator would be a consistent heat source. However, this method would not account for the rate at which blood is rubbed off of eggs during the course of incubation. Another plausible experiment would be to wash eggs during the first few days of incubation. However, important factors would have to be taken into consideration, such as using a liquid to wash an egg in a cold climate and the fact that this would likely have to be done daily for a period of at least a week to take into account variations in nest initiation and continual blood deposition by fleas.

If a decrease in nest success was attributed to female behavior, alterations in female behavior would be the ultimate cause of nest failure, with the proximate cause likely being either cold-induced embryo death likely due to nest abandonment or increased predation due to the possibility of longer breaks by females that experienced flea-induced annoyance. It is not possible to determine whether eggs failed due to nest abandonment or predation at the Karrak Lake colony as nest that have been abandoned are likely to have been depredated after abandonment.

Although there are endless questions about a system recently discovered, here are a few questions I propose for future studies:

- 1) Habitat variables measured in this study only described 10% of the variation in flea abundance, what variables that were not measured may describe more of the variation?
- 2) What is the exact life-cycle of fleas in the Karrak Lake colony and what are their survival constraints?
- 3) Is goose body condition affected by flea abundance?
- 4) Is there a difference in age distribution between infested and un-infested geese?
- 5) Do infested geese illicit an immune response? If so, are there costs for geese and/or implications for fleas?
- 6) Will fleas infect other avian species in this colony?

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